

III. *On the phylogenetic significance of the wing-markings in certain genera of the Nymphalidæ.* By FREDERICK A. DIXEY, M.A., M.B., Fellow of Wadham College, and Demonstrator in the University Museum, Oxford.

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PLATES I., II. & III.

EVERYONE who has paid any attention to the perfect insects of the genus *Vanessa* and allied forms, must have been struck with the great general resemblance that exists between them in respect of their wing-markings.* In the investigation of which I now present the results, my first object has been to ascertain the exact extent of this resemblance by analysing the wing-patterns and reducing their constituent markings to a system; from this I have been led to search for homologues of the markings in certain other members of the family *Nymphalidæ*, and finally to use the interesting conclusions thus arrived at in an attempt to sketch the outline of a phylogeny for insects of the genera examined.

I need hardly point out that facts of the kind here dealt with, relating, that is to say, entirely to certain special external characters of adult forms, constitute only one kind of phylogenetic evidence out of many that could be brought; and that conclusions resting on them, though valuable as contributions towards the settlement of the question of kinship, must not be held to be final unless they are corroborated by the result of other lines of enquiry—especially those relating to the ontogeny of the various species concerned, and to their distribution in space and time.

* See a note in Weismann's 'Studies in the Theory of Descent' (English Edition, 1882, vol. ii., p. 447), by Prof. Meldola, who observes, "The genus *Vanessa* (in the wide sense) appears to be in a remarkable condition of what may be called phyletic preservation."

Moreover with reference to the study of these markings in especial, it must not be forgotten that the investigator is deprived of the assistance usually afforded to similar enquiries from the side of embryology, for the characters in question spring as it were at once into perfect being at a definite stage in the life of the individual; they have, so to speak, no growth, no embryology.* Nevertheless, in spite of these limitations, it would seem worth while to examine the evidence available from this source with as much accuracy as possible, to see how far it will go towards indicating lines of probable development, and to determine the direction in which such lines appear to lead. The conclusions so reached will no doubt need to be checked and corrected by evidence derived from other quarters, but ought, nevertheless, to be allowed their due weight in any settlement that endeavours to be final.

The amount of material available for the construction of a phylogeny of the *Nymphalidæ* as a whole has received a notable addition in an elaborate memoir by W. Müller ('Südamerikanische Nymphalidenraupen'), published in the 'Zoologische Jahrbücher,' Bd. I., 1886, pp. 417—678. His conclusions, however, as there given, extend in the main only to groups of higher importance than genera; and the sole data on which they rest are the facts of the larval and pupal ontogeny and habits, the perfect form being left out of account altogether.

In comparing the evidence of kinship derived from the study of immature stages with that obtainable from adult forms, it must not be forgotten that in cases such as the present, in which the immature stages have a separate and independent existence of their own, the conditions amid which the earlier periods of life are passed will have their own special influence upon the larval form and development, without necessarily producing any corresponding effect upon the form ultimately assumed; and that consequently the affinities disclosed by the larva do not always exactly correspond with those indicated by the perfect organism. This point, to which attention had in some degree been

* A possible exception to this general statement may exist in the pigmentation of the wings of certain pupæ. This point needs further investigation. See below, pp. 125—128.

previously directed by Darwin* and Lubbock,† has been fully treated of with great completeness of illustration by Weismann, in his essay on 'Phyletic Parallelism in Metamorphic Species,‡' where he has shown this want of congruence between larval and imaginal affinities to be especially well-marked among certain of the sub-groups of the family now before us. In cases where the form-relationship of the larvæ does not coincide with that of the imagines we may find it difficult to determine which of the two is the more trustworthy guide to the real affinities of the species; but where the evidence from both sides can be shown to point in the same direction such grounds of doubt no longer exist, and we may claim to have gone far towards establishing the true phylogenetic relation. It is interesting therefore to find, as will appear before the end of this paper, that Müller's conclusions, as far as they go, and when due allowance is made for the facts just referred to, are in general accordance with the results to which I have been led by an entirely distinct method of investigation.

As a preliminary to the minute comparative study of the wing-markings, it will be well to lay down certain landmarks to serve collectively as a sketch outline of which the details may be afterwards filled in. For this purpose let us first of all glance at the costal margin of the fore wing in *V. urticae* (fig. 1). Here occur three dark patches alternating with four areas of lighter ground colour, the innermost of which is red, the next two yellow, and the outermost white. These three dark patches I distinguish by the Roman numerals I., II., III., in order from within outwards; while to the four light coloured areas I give in similar order the letters A, B, C, D. Outside the white patch D comes the dark sub-marginal band. This I regard as in series with the costal patches, and accordingly recognise it as IV. Now these eight costal areas of alternate light and dark colour will be found in one form or another in most of the insects with which we shall have to deal; and I

* 'Origin of Species,' p. 440 (1st Edition).

† 'Origin and Metamorphoses of Insects,' 1874; vid. esp. pp. 89, 70.

‡ 'Studies in the Theory of Descent,' English Edition by Prof. Meldola, 1882, vol. i. p. 390—vol. ii., p. 554.

therefore propose to adopt the letters and numbers I have just given as a uniform means of distinguishing these markings both in figures and descriptions. In certain forms, as for instance *V. polychloros*, *V. io* (fig. 2), and the various species of the genus *Grapta*, they are as easily recognised as in *V. urticæ*; in others one or more may be obliterated (as A in *P. atalanta*, see fig. 3), the rest remaining easily recognisable; in others again some or all of the patches may be broken up into separate constituents, as in most members of the genus *Argynnis* (fig. 4), but, as will be shown, not in such a way as to lose their actual identity. When this resolution happens, I shall retain the letter or number already given as the collective designation of the entire group of constituent markings, while generally distinguishing the separate members by the Arabic numerals, 1, 2, 3, 4, &c., in the case of the dark, and the letters α , β , γ , δ , &c., in the case of the light areas. It will be seen in the sequel that in nearly every case the costal patch forms part of a series of markings which belongs or did belong to the entire wing, and indeed to both fore and hind wing alike. It will therefore be necessary, as we proceed, to enlarge the notions we have at first attached to the letters A to D, and the numbers I. to IV., and to make them stand for the whole range of marks, of which the most conspicuously and uniformly recognisable portions occupy the region of the costa. It will, moreover, in some cases be convenient to introduce a further division of groups into II. and II', III. and III', &c. (figs. 31, 37).

We may now begin the consideration of the wing-markings in detail, taking first—

1. *The series of light-coloured spots near the apex of the primaries.* — Comparing *Pyrameis cardui* with *P. atalanta*, we are at once struck with the identity of pattern shown by the apex of the fore wings in these species. On the black ground of this region in *P. cardui* occur four conspicuous white spots (fig. 5, α , β , γ , δ) arranged in a curve, the first and fourth being markedly larger than the other two. These are obviously homologous with the similar white spots in *P. atalanta* (figs. 6, 7), which are arranged in a curve of the same character and keep much the same relative size, β and γ being, however, a little smaller in *P. atalanta* than in *P. cardui*, and α showing distinctly

in the former species the crescent shape only indicated in the latter.

In *P. atalanta*, however, we find that the series does not end with no. 4, which we have called δ . There is in this species always present a fifth spot, continuing the curve, and in the female a sixth as well* (figs. 6, 7, ϵ , ζ); this last spot, a very small one, coming within the red band of the fore wing. Now the first of these spots obviously corresponds with the white costal patch in *V. urticae*, which I have called D. I shall continue, therefore, to refer to the six spots under the names of the first six letters of the Greek alphabet, α , β , γ , δ , ϵ , ζ , speaking of them collectively as series D.

Although in the great majority of specimens of *P. cardui* only the first four terms of this series are represented, yet it sometimes happens that the fifth, and even in rare cases the sixth, is present as well. A specimen of *P. cardui* was caught at Morteheo, North Devon, by Miss Daisy Longstaff, in the autumn of 1889 (fig. 8), in which ϵ is as distinct as in *P. atalanta*. Two specimens in the Hope Collection at Oxford show the same peculiarity; one being British, the other from North America. In most of these cases the spot is larger on the under surface of the wing than on the upper.†

On the other hand, in *P. huntera* and *P. myrinna*, which bear a general resemblance to *P. cardui*, I have never seen ϵ ; but ζ is always present and usually very conspicuous (fig. 9).

In all other species of the genus *Pyrameis* the series is present in greater or less completeness. The spots most constantly present are α and δ . In those members of the group that approach *P. atalanta* in aspect, β and

* A specimen in the British Museum has this sixth spot on the left side and not on the right. Scudder, in his 'Butterflies of the Eastern United States,' 1889, does not notice this spot either in his description (vol. i., p. 442), or figure (vol. iii., pl. 2, fig. 6). The latter is expressly said to be of *P. atalanta* ♀.

† A third specimen of *P. cardui* in the Hope Collection shows the whole range from α to ζ ; ζ is here well marked on the under-surface, but on the upper only faintly indicated, — being, indeed, reduced to a few scales of lighter shade than the general ground colour. A specimen in the British Museum resembles the Morteheo specimen in the presence of ϵ , but differs from it in another respect; see below, p. 113.

γ (especially β) tend to become small and to disappear; ϵ is mostly present (small or absent in *P. callirrhoe*, fig. 10); ζ as a rule is absent, except as we have seen in *P. atalanta* ♀. In those that approach *P. cardui*, i.e., the assemblage of species distinguished by Scudder* as "Neopyrameis," β & γ are tolerably conspicuous, ϵ nearly always absent, but ζ may be very large and distinct, as in most specimens of *P. huntera*. *P. gonerilla*, from New Zealand (fig. 11), has α — ϵ constantly and plainly present, their appearance being, however, modified by an invasion of blue, the meaning of which we shall see later.

A careful examination of the whole family *Vanessidæ* and allied groups shows that this series D, α — ζ has a very extensive range; though in passing away from the insects just specially referred to it in most instances soon begins to lose its distinctive and conspicuous character.

At first, however, the series is plain and recognisable enough. *V. io* (fig. 12) shows the whole set complete from α to ζ ; α is here coloured pale yellow, and is modified in shape in order to form the outer part of the pale zone of the eye-mark; δ though preserving its relative size is elongated conformably with the outline of the same mark, and all the spots from β to ζ are invaded by a pale blue colour, the meaning of which, like the somewhat similar feature in *P. gonerilla*, will be considered later.

In *Araschnia levana* we have the same series; α , δ and ζ being the most constant members, while γ & ϵ are small or absent. In the dark form known as *A. prorsa*, however, all are usually present (figs. 13, 14).

Other well-marked cases of the complete or partial presence of the series are afforded by *Eurema zabulina* (α and δ), *E. kefersteinii* (α , δ , ϵ , sometimes γ , underside α — ζ), *E. dione* (α , [γ],† δ , ζ). In this latter case the spots α — ϵ on both upper and underside are silvery, while ζ is vertically elongated and transparent. The assertion that the window-slit in the centre of the fore wing in *E. dione* represents the minute white spot in the red band of the female *P. atalanta* may sound far-fetched and unlikely to be true, but to any one who will

* Op. cit., vol. i., p. 434.

† Sometimes absent.

compare the following—*E. dione*, *E. kefersteinii*, *P. huntera*, *P. atalanta* ♀, there will be no possible doubt of the correctness of the identification (figs. 15, 16, 17).

In *V. polychloros* (fig. 18), the spots of this series are of a reddish yellow, not very far removed from the orange-brown ground colour of the wing; nevertheless it is usually easy to identify α , β & γ . The rest of the series is less readily made out; however, in some specimens δ , ϵ and ζ are to be distinguished, and even a further member which we may call η .

V. urticae, as we have seen, has α well developed and pure white in colour, but no further members of the series are present.

In *V. antiopa*, α and β are conspicuous and fused; γ and δ are faintly visible in some specimens, both on the upper and under side.

The same series of spots may, perhaps, be traced in the genera *Apatura* and *Limenitis*. If we compare the fore wing of *Apatura iris* with that of *Vanessa atalanta*, we cannot fail to be struck with the general resemblance of the pattern at the apex in the two cases, though whether the outer series of white spots in *A. iris* really corresponds with that in *V. atalanta* seems doubtful. Spots, however, more or less answering to β , γ and ϵ , are easily recognised in the male *A. iris*, while in the female α and δ are possibly present as well (fig. 19). There is, however, a certain departure from the *Vanessa* and *Pyrameis* type, in respect of the arrangement and relative size of the spots. Thus, β and ϵ are relatively large in *Apatura*, small in *Pyrameis*; moreover in *A. iris*, ϵ though preserving the same relation to the nervules of the wing as in *Pyrameis* and *Vanessa*, seems as far as the pattern is concerned to have stepped into the place of δ .

In *L. sibylla* we find the series present in *A. iris* verging towards disappearance. It is not difficult, however, to identify α , and probably β and ϵ (fig. 20).

But the most interesting results in connection with this series follow from tracing it in another direction. The general uniformity of pattern in the genus *Argynnis* is well known, and at first sight it may seem that these insects present nothing that corresponds to this series of spots. If, however, *A. valesina*, the melanic variety of the female of *A. paphia* (which probably represents a

reversion to, or survival of, an ancestral type) be carefully examined, it will be seen that the arrangement of dark spots and pale ground colour near the tip of the fore wing closely corresponds with the pattern we have been considering in the *Vanessidæ* (figs. 21, 27; cf. figs. 1—4). This correspondence is strikingly brought out in some specimens by the creamy white colour of those pale areas that answer in position to the dead white band and spots in *P. atalanta*, the rest of the ground colour of the wing in *A. valesina* tending to a dusky olive.

The *Vanessa*-like character of this region of the fore wing, which as we have just seen is perceptible enough in the dark variety of *A. paphia* ♀, becomes remarkably vivid in the female of *A. niphe*; so much so, in fact, as to give the latter insect almost the general aspect of a *Pyrameis*, the underside especially suggesting that of *P. cardui*.* The resemblance does not depend only on the special points which we are now considering, but also on other features which will be noticed later. Confining our attention for the present to the series D, α — ζ , and making a careful comparison between *P. cardui*, *P. atalanta* ♀ and *A. niphe* ♀, we shall not be able to escape the conclusion that the series is exactly represented in this last insect, spot for spot (fig. 22). The only apparent exception is ζ , which is often absent from the upper side of *A. niphe*; on the under side, however, ζ is distinct and conspicuous, and in at least one specimen that I have seen (Hope Collection) it is faintly visible on the upper side as well. The comparison of *A. niphe* ♀ with other members of the genus *Argynnis* makes it clear that these light-coloured markings, which I have shown to be homologous with the white spots of the *Vanessidæ*, are merely an accentuation, as it were, of the general ground colour of the wing between certain of the dark spots which are so characteristic of the *Argynnidæ*.† If any doubt remains

* The aspect of *A. niphe* ♀ is no doubt partly the result of its mimicry of *Danaüs chrysippus*, but the special points named here and below (p. 101) can scarcely be affected by this fact. Moreover the resemblance as a whole is seen, on careful comparison with other *Argynnids*, to depend on the retention and intensification of true *Argynnid* characters, not (with the exception, perhaps, of the general shape of the wings) on the acquisition of new ones.

†The spot α is in one respect exceptional, as will be seen later (p. 101, note). It is to be observed also that the white spots in *A. niphe*

on this subject, it will be removed by a comparison of *A. sagana* ♀, *A. niphe* ♀, *A. valesina* and *A. diana* ♀ with *C. pantherata* and with the male of almost any *Argynnis* that it is most convenient to take; for instance, *A. adippe* or *A. paphia*. Putting together the results of the examination of all the insects that have been referred to, we recognise the areas between the dark spots of this region of the fore wing in the *Argynnidae* (seen perhaps in their simplest form in *A. diana* ♀), as in most instances simply partaking of the usual brown ground colour of the wings (*A. adippe*, *A. paphia*, &c.), in other instances becoming somewhat specially marked out by an increase of paleness (*A. valesina*, *C. pantherata*), and in *A. sagana* ♀ and *A. niphe* ♀ assuming the character of a system of definite spots; which character becomes absolutely established in *Vanessa*, *Pyrameis*, *Araschnia* and *Eurema*, perhaps passes over in a modified form to the genera *Limenitis* and *Apatura*, and beyond these limits gradually loses its distinctive features and disappears. That the homology of the spots in all these cases (except the last) is perfect there can be little or no doubt for any one who will carefully examine the insects named. That the true line of development has been indicated in the above account is more open to question; it will, however, be seen in the course of this paper that the conclusion here arrived at is corroborated by other evidence.

2. *The submarginal chain of black spots with blue centres*.—I now wish to call attention to another feature in the colouring of the *Vanessas* and allied genera, and in the same way to make an attempt to trace its history. Near the anal angle of the hind wing in *Pyrameis cardui* there occurs a long narrow oval or crescentic black spot with a blue core or centre, the latter often showing signs of a division into two* (fig. 24, IV., 15). This spot is

are not absolutely distinct and circumscribed as in *P. cardui* and *P. atalanta*, but represent merely the central portions of small areas of unaltered ground colour into which they shade off with greater or less gradation of tint. In the genus *Pyrameis* the original ground colour has disappeared from around the spots α to ϵ , persisting only in the neighbourhood of ζ .

*This duplication of markings in the space between the submedian nervure and 1st median nervule is a common feature in both fore and hind wings of many species. See especially the blue spots in *V. urticae* and *V. antiopa*. (Fig. 26, IV., 8, 15).

evidently the last term in a series of dark spots which forms a kind of inner border to the hind wing, there being a separate oval or diamond-shaped spot for each interspace between the nervules with the exception of the first two or three interspaces, in which the spots of this series are fused together (fig. 24, IV., 10—15). In *Pyrameis atalanta* the same blue-centred spot occurs in the same situation, and here again it is easily seen to be the last term in a series. But in *Pyrameis atalanta* the blue colour is not confined to this last term, for in most, if not all, specimens a definite area of blue, varying from a few blue scales to a well-marked patch, occupies the centre of the last spot but one. In the hind wing of *V. polychloros* we recognise at once the same submarginal series of spots, forming a complete inner border to the wing, each spot being now crescentic in outline, more or less fused with its neighbours, and the blue centre being found not only in the last one or two terms of the series, but in all of them except the first. The inner portion of the border of the fore wing in *V. polychloros* is formed by an evident continuation of the same series, visible also in the fore wings of *P. cardui* and *atalanta* (especially in *P. cardui*, under side), but in these latter cases somewhat obscured by the general coloration of the dark area of the wing. The series as a whole is that which we have already distinguished as IV., and the anterior portion of which forms the external boundary of the light-coloured series D, α — ξ . The conspicuous blue centres of the marginal spots in the hind wing of *V. polychloros* do not extend to the remainder of the series in the fore wing; nevertheless, in many specimens a few blue scales, quite inconspicuous, may be detected in the centres of IV., 5, 6 and 7. The same blue-centred chain of submarginal spots is very plainly visible in *A. levana*, especially on the upper surface. It occurs with great distinctness on the under surface of *A. prorsa*, and as a trace at the anal angle of the hind wing on the upper surface of the same insect, as also in *P. gonerilla* (fig. 25, IV., 15). Similar traces will be found at the anal angle of the hind wing in *E. kefersteinii* (best marked on under surface), and *E. dione*, in these cases the blue being reduced to a few blue scales, almost invisible to the naked eye. If we now turn to *V. urticae*, and notably to *V. antiopa* (fig. 26),

we find the whole series of black submarginal spots with their blue centres complete and conspicuous. In the latter insect the crescentic outline of the spots, constant in *V. polychloros*, is mostly lost; and the spots become fused into a black band easily distinguishable from the dark chocolate colour of the general surface of the wing. An indication of the formation of this band by the fusion of separate members, each corresponding to an interspace, is preserved both by the crenated outline of the band and also by the blue centres, which in this species are large and conspicuous, their outline tending to become roundish or oval. The character of this submarginal band or chain of spots in *V. urticæ* bears a strong general resemblance to the same in *V. polychloros*, but in *V. urticæ* the distinct development of the blue centres in the upper wings marks an approximation to the condition in *V. antiopa*, which is also borne out in some specimens by a tendency towards complete fusion of the black spots, and the substitution of an oval or roundish outline for the crescentic shape of the centres.

Having now examined this system of blue and black markings in its almost evanescent condition in *P. cardui* and *P. atalanta*, and its state of greater development in *V. polychloros*, *A. prorsa* and *levana*, *V. urticæ* and *V. antiopa*, we will glance at two or three species closely allied to those mentioned, in which we shall find it represented under curiously modified forms; and then proceed to consider whether there is any evidence which may throw light upon its history.

If anyone will attentively examine the tip of the fore wing in *V. io* and compare it with the same region in *V. urticæ*, he will not be long in coming to the conclusion that the black crescent with its included blue area, which forms the outer portion of the ocellus in the former species, is the exact representative of the first part of the submarginal series which we have been considering in *V. urticæ*. It has been already pointed out how the spots D α — δ are modified in *V. io* in order to help in the formation of the ocellus; the same applies to the present series. The first part of the series remains, the black spots being fused into the outer crescentic region of the ocellus. The blue centres are in some specimens quite separate, and easily to be identified with those of IV., 1—5 in *V. urticæ*; in many, how-

ever, they are fused, though seldom without retaining clear indications of their separate nature. Although the black constituent of this submarginal series (IV.) ceases to exist as a conspicuous feature behind the region of the ocellus, a relic of it can be detected in most, if not all, specimens in the form of a small dark patch just outside the spot ϵ , with a few blue scales to indicate the blue centre.

On page 94 attention was called to the invasion of the spots D β — ζ in *V. io* by a blue coloration. This affects both the spots themselves and the surrounding area of the wing, the scales composing the spots being not quite white, but a very pale blue, and the surrounding areas having scales of a blue nearly or quite as intense as that of the blue centres 2, 3, 4, plentifully mixed with other scales that merely present the bright chestnut of the general ground colour of the wing. This last feature in the colouring I shall speak of as the "blue shade." Its appearance in *V. io* irresistibly suggests the inference that it is due to an extension inwards of the blue of the centres of the fused submarginal spots, and this is put almost beyond doubt by a comparison of the corresponding region in *P. atalanta*, *P. huntera*, and *P. gonerilla*.

As has been before mentioned, the submarginal black band is quite recognisable in the fore wing of *P. atalanta*, though to some extent masked by the general black colour of the wing. We have seen that the blue centres are represented at the anal angle of the hind wing. But they are also represented in the fore wing, in some specimens with great distinctness, by two or three crescentic blue patches in the black ground colour, just outside the spots β , γ , δ , ϵ ,—nearly the same situation, in fact, as the blue centres that survive in the fore wing of *V. polychloros*. These blue crescents, though usually well outside the white spots, in some cases approach them closely, and may even encroach upon δ , as in a specimen in the Hope Collection. We have only to turn to *P. gonerilla* to see this encroachment carried to a much greater extent. Here α is bordered with blue on its outer side, δ has a narrow blue band surrounding it, expanding externally to a broad blue margin; β , γ and ϵ are blue altogether.

I have only once seen anything of the kind in *P. cardui*,

but β and γ are nearly always blue, or at least edged with blue, in *P. huntera* and *P. myrinna*.

These cases would seem to support the suggestion already made that the "blue shade" in *V. io* represents an encroachment inwards of the blue of the centres of the submarginal series of spots.*

The question now arises whether we can trace the origin of this series of blue-centred spots, which we have seen in their full development and in their decline. It will be understood how keenly, when I was investigating this point, I sought among the Fritillaries for some indication of this blue-centred black border. Did there exist any species of *Argynnis* with blue round the margins of the wings? The clue to the solution of the question was supplied by the same species that is of so much interest in regard to the series D, α — ζ , viz., *A. niphc*. In this insect we are at once struck by the resemblance of the hind wing, both in σ and ρ , to that of *P. cardui*. The various series of dark markings are seen to correspond, spot for spot, and what is more interesting still, the submarginal portion of the wing shows a blue colour, best developed near the anal angle, which at once suggests the remnants of blue in *P. cardui*. The blue here does not, it is true, occupy the centres of the dark spots corresponding to those which form the submarginal series in *P. cardui*, but rather belongs to the ground colour between this series and one still further out, while externally comes another interrupted narrow area of blue ground colour before the black edge of the wing is finally reached. Still it is difficult to resist the conclusion that the blue in *P. cardui* is derived from a source indicated by the same colour in *A. niphc*, which indeed may have been effected by a spreading inward of the blue in the form of a shade which has afterwards been cut off, of which we have already seen an example in *A. prorsa*, or by the taking up of the outer row of dark spots in an attenuated form to make with the submarginal row a series of composite spots, the included blue ground colour becoming the centres of the series so made. This

* A similar extension inwards of bluish coloration from the series of blue-centred spots occurs on the under side of *A. levana*, both upper and lower wing. In *A. prorsa* (hind wing) this has become separated from the border, remaining as a small but distinct bluish patch.

last is most likely the true explanation, if indeed it is not put beyond doubt by a comparison of the anal angle, under surface, of *A. niphe* with the same region, either upper or under surface, in *P. atalanta*.

A comparison of the upper wings in *A. niphe* ♀ and *P. atalanta* gives a similar result. The submarginal series IV., very distinct in *A. niphe*, as in nearly all species of the genus *Argynnis* (fig. 31), is sometimes indicated in *P. atalanta* with tolerable distinctness, especially in its upper part, and is here seen to be bounded outwardly by an interrupted bluish area like that which in *A. niphe* bounds the same series of spots, though it is less conspicuous than in the hind wing. Further along the margin of the wing in *P. atalanta* the same interrupted bluish area occurs, and is here reinforced by a few scales of a more intense blue, which, as we have seen, spread inwards over the centres of the fused dark spots of IV., forming a "blue shade" like those already mentioned, and even reaching and encroaching on the white spots of series D, α — ζ . There can, I think, be little doubt of the substantial identity of series IV. in these two species.

A. niphe, as far as the arrangement of the black spots on the ground colour is concerned, is quite a typical *Argynnis*; and this particular series (IV.) runs in a very well-marked form throughout the genus (fig. 27, &c.). As far, then, as the first constituent of the series of marks we are considering is concerned, *i.e.*, the submarginal chain of black spots, we find it well-established in the Fritillaries, and persisting in a more or less marked degree in the Vanessas. There would seem to be little doubt that, as in the case of the series D, α — ζ , we have in *Argynnis* the generalised or ancestral and in *Vanessa* the specialised or derived form of the series, and this conclusion is supported by a further investigation into the history of the second constituent, *viz.*, the blue centres and shades. If we are right in tracing back the blue centres to the indications of blue ground colour in *A. niphe*, it becomes important to ask, What is the meaning of the latter?

Now it is a well-known fact that in very many species of *Argynnis* the two sexes differ in colour, one being much darker than the other. When this is the case the darker is invariably the female. The general darker appearance is partly due to the larger size of the black

spots (*A. paphia*), partly to an alteration in the general ground colour, which in these females shows an infusion of a dull olive of various degrees of intensity into the bright tawny ground colour characteristic of the male (*A. paphia*, *aglaia*, *adippe*, &c.). As is well known, a "melanic" variety of the female of the first-named species sometimes turns up, in which the whole ground colour is of a deep dusky olive, no trace of the usual tawny colour being visible. The females of some species of *Argynnis* are normally as completely destitute of the usual bright ground colour as these occasional melanic females, the prevailing tone in such cases being, similarly, a deep dusky olive or blue-green; the bluish tinge prevailing, *e.g.*, in *A. diana*, the greenish in *A. sagana*. In other species we see this dark blue or green ground colour confined to a particular area of the wing, *e.g.*, the tip of the fore wing and border of both wings in *A. niphe* ♀, the border of the hind wing in *A. niphe* ♂; the posterior and inner half of the hind wing in *A. pandora* and *A. childreni* ♀, the border at the anal angle in the hind wing of *A. childreni* ♂. It is significant that in all these cases, if the bluish or greenish ground colour is visible in only one sex, that sex is the female; if it is visible in both sexes, it prevails to a much greater extent in the female than in the male.

Prof. Meldola (in Weismann, *op. cit.*, vol. i., p. 8, note) quotes Mr. Wallace* as holding that the dark colour of many female butterflies is a character acquired for purposes of protection; but the facts to which I have called attention, more especially the occasional occurrence in at least one brown *Argynnis* of a melanic variety so closely resembling in coloration the normal female of other species, and the presence of traces of the same dark ground colour in some of the male *Argynnis*, would seem rather to point to the conclusion that at any rate in this group the dark blue or green is ancestral; preserved, no doubt, in many instances for purposes of protection, but in the first place deriving its origin from the progenitors of the race.

* 'Contributions to the Theory of Natural Selection,' 1870, pp. 112—114. In the same author's 'Darwinism,' 1889, pp. 276, 277, the analogous sober coloration of the female in many species of birds is considered to be an ancestral rather than an acquired feature. I am not sure that Wallace's words as cited by Professor Meldola necessarily imply that the same may not be the case with butterflies.

The melanic females would then be instances of reversion or survival, and the whole aspect of the females of the genus would be a case of the well-known rule that in species where sexual dimorphism or "antigeny" occurs, the female most nearly approaches the ancestral type, the male being the more highly specialised form.* The nearest representative of the primitive *Argynnis* would thus seem to be the female of *A. diana*, and it is interesting to note that one of the earliest butterflies yet found in a fossiliferous deposit† belongs apparently to that species, or at least is not easily to be distinguished from it. The first step in specialisation we may imagine to have been already taken in *A. diana* by the lightening of the ground colour in certain places, leaving darker patches forming a chain of spots. A further extension of the same process would give us a form like the melanic *A. paphia* (*valesina*), or, if a marked accentuation of some of the lighter areas took place, the female *A. sagana*. The bright fulvous ground colour of the majority of *Argynnis* would then represent a still further advance in specialisation, affecting, as we should expect, chiefly the males; and in such instances as

* Scudder (*op. cit.*, vol. 1, p. 533) maintains that in these cases it is the *female* that departs from the general type, though he admits that this is "precisely the opposite conclusion to that reached by Darwin." He quotes the case of *Scnuopsyche* (*Argynnis*) *diana* ♀ as an instance of complete departure from the ordinary colouring of the group, but makes no mention of such similar colouring as is visible in *A. sagana* ♀, *A. niphe* ♀, *A. valesina*, &c. The partial dark coloration of certain males he accounts for by saying that "in other cases the melanic feature has been superinduced upon the opposite sex" (vol. 2, p. 951). It does not, however, seem to me that he has given sufficient reasons for his view to ensure its general adoption; and indeed the following passage would not appear to be in accordance with his own opinion as elsewhere expressed:—"Some species, which we can hardly doubt have had a common ancestor, scarcely differ from each other excepting in the character of their antigenic peculiarities, and this accounts for the close resemblance of the females of allied species of Skippers" (Ib.). Surely this must mean that the males are the more specialised. A good instance of the preservation of an ancestral character by the female alone is afforded by the spot ζ in *P. atalanta* ♀, as noticed above, p. 93. With respect to the alleged mimicry on the part of *A. diana* ♀, which forms part of Scudder's argument, see note on pp. 105, 6.

† "*V. pluto*" of Heer, from the Oligocene of Radaboj, Croatia. Vid. Lyell, *Elem. Geol.*, 1885, pp. 214, 5; Edwards, *Butterfl. N. Amer.*, 1879, vol. i.

A. niphe ♂ and ♀, *A. childreni* ♂ and ♀, &c., we should recognise the last battle-ground between the rival tints, the old one holding its own longest in the female, and especially clinging to the region of the borders and anal angle of the wings.*

If this be the true account of the bluish or greenish areas in the wings of such species as *A. niphe*, and if this survival of the ancestral ground colour about the borders of the wings be the origin, as seems most probable, of the blue constituent of series IV., so constantly present in the *Vanessidæ*, we have in the whole history of this series of markings an interesting case of the revival and fresh employment of an almost obsolete feature; just as if an old weapon, rusty from disuse, were polished up anew and once more turned to account, not indeed for its old purposes, but as a piece of ornament. The history of the series D, α — ζ , we saw to be somewhat similar, inasmuch as they represent mere lighter areas of ground colour, seized upon as it were and turned to more distinctly decorative purposes. In the two cases the most probable lines of origin are seen to converge from the showy and highly specialised *Vanessas*, through such forms as *A. niphe* to the archaic and comparatively sombre female *Argynnis diana*.†

* Perhaps even in this diminished form still serving as a protection, by shading the insect off against its surroundings, when sunning itself in the usual manner of Argynnids.

† Scudder ('Butterflies of the Eastern United States,' 1889, pp. 257, 532, note, 718, 1802, &c.) asserts that the difference between the sexes in *Semnopsyche* (*Argynnis*) *diana* is due to mimicry; the female *A. diana* mimicking *Basilarchia astyanax* (*Limenitis ursula* of Doubleday and Westwood). "There can be no doubt," he says, "that *S. diana* is the mimicker, since it obtains its resemblance by departing from the ground colour not only of the opposite sex, but that prevailing in both sexes in the whole tribe of Argynnidi to which it belongs." I do not find myself able to concur with Scudder in this opinion, for the following reasons:—(1). The ground colour of *A. diana* ♀ does not widely differ from that of many other female Argynnids, e.g., *A. valesina*, *A. sagana*, and (for part of the wing) *A. niphe*. There is therefore no need to assume mimicry in order to account for it. (2). The habits of *A. diana* are not those of an insect protected by mimicry, it being, according to Edwards, "an exceedingly alert and wary insect." (3). The resemblance of the two insects is not close. *A. diana* is much larger than *B. astyanax*, and differs widely from it in shape. (4). On the other hand, there is a close resemblance, as pointed out by Doubleday and Westwood ('Genera of Diurnal

3. *The white band on the costal margin of the fore wing.*—Returning now to *P. cardui* and *P. atalanta*, we find another conspicuous mark near the apex of the fore wing besides those already noticed. This is the broad white band passing inwards from the costa at the junction of its outer and middle thirds, to which I have already given the distinctive letter C. No question can possibly arise as to the identity of C in these two species.

Lepidoptera,' vol. ii., p. 275), between *B. astyanax* and *Lærtias* (*Papilio*) *philenor*. This resemblance extends not only to markings and colour, but to form and size as well. It is noticed by Scudder (*op. cit.*, p. 287), but dismissed as insufficient to establish mimicry. (5). The genus to which *B. astyanax* belongs contains undoubted cases of mimicry in which the *Basilarchias* are the mimickers. This raises a presumption in favour of *B. astyanax* mimicking rather than being mimicked, which is strengthened by the fact that *B. astyanax* has scarcely the aspect of a typical *Basilarchia*. (6). In favour of the view that *B. astyanax*, whether mimicked by *A. diana* or not, itself mimics *L. philenor*, are the facts given by Scudder (vol. ii., p. 1251), on the authority respectively of Edwards and Doubleday, that the latter butterfly "has a strong and disagreeable scent," and that "its flights are rather low and not very powerful." It would therefore seem that *L. philenor* is specially protected, and that it would be advantageous to another insect, such as *B. astyanax*, to be mistaken for it. On the other hand, no reason is alleged by Scudder why it should benefit *A. diana* to be taken for *B. astyanax*, nor does he suggest that *A. diana* may be taken for *L. philenor*. (It should be stated that Scudder fails to verify the point as to the evil odour of *L. philenor*.) On the whole, therefore, it seems to me that the evidence of mimicry between *L. philenor* and *B. astyanax* is much stronger than that between *B. astyanax* and *A. diana*; and if, as Scudder thinks, the former is insufficient, *a fortiori*, the latter must be also. I should wish, however, to point out that even if it be conceded that *A. diana* ♀ is a mimicker, it does not follow that the ground colour was acquired for that purpose; it may merely have survived. Moreover, the spots of *A. diana* ♀ are those of a typical *Argynnis*. The blacking-in of the base of the wings internal to series II. has its counterpart in other American *Argynnis* (*A. cybele*, *A. nokomis* ♀, and especially *A. leto* ♀), and the only character that, so far as I know, is really peculiar to *A. diana* among its relatives is the large expanse of blue ground colour surrounding the spots of series III., which I admit to be like the corresponding feature in *B. astyanax* and *L. philenor*. Whether, therefore, such resemblance as exists between these insects be due to mimicry or not, I see no reason to doubt that *A. diana* ♀ is a near representative of the oldest type of the *Argynnis*, and so in all probability of the *Nymphalidæ* generally. I may add to the above that Mr. Wallace, in his lately published volume 'Darwinism,' 1889, p. 248, speaks unhesitatingly as to the mimicry of *P. philenor* by *L. ursula* (Scudder's *B. astyanax*), but makes no mention in this connection of *A. diana*.

They correspond exactly, and C is also recognisable with equal certainty in very many of the allied species, e. g., *P. huntera*,* *P. gonerilla*, *P. callirrhoe*, &c. (see figs. 5—11). In *Araschnia prorsa* and *levana* C is again to be seen, in the former as a conspicuous pale yellow band, in the latter as a portion of the light ground colour of the wing between the dark areas II. and III. A similar condition obtains also in *Vanessa urticæ* and *V. polychloros*, in both of which C begins on the costa as a yellow band, which as it passes inwards soon becomes merged in the general reddish brown ground colour, this happening earlier in *V. polychloros* than in *V. urticæ*. In *P. carye* C is distinct and circumscribed, and of the same colour as the general surface of the wing. A relic of C is visible in *V. antiopa*, and in *V. io* (fig. 12) the band is present and modified to form the pale zone of the inner side of the ocellus, being in this species of very nearly the same pale yellow as in *V. urticæ*. Many other allied forms (e. g., the genera *Grapta* and *Eurema*) show C with greater or less distinctness, and it is interesting to observe that it passes over into the genera *Limenitis* and *Apatura*. *L. sibylla* and *A. iris* both exhibit it very plainly (figs. 19, 20). In these two insects it passes by one interspace further into the wing than in most specimens of *P. cardui*, but some specimens of the latter show a paling of the ground colour in the situation corresponding to this extension, which becomes more marked on the under side; and in European, though not in American, specimens of *V. atalanta* a small white projection is constantly present in the same place.† Can an origin be assigned for this band C with the same amount of probability as in the former cases? Again we look to *Argynnis niphe* ♀ for an answer to the question. In this insect C is as distinct and conspicuous as in any *Pyrameis* or *Vanessa*, and is plainly seen to be an accentuation of the ground colour between the chain

* According to Scudder (*op. cit.*, vol. i., pp. 430, 458) C is white in the male *P. huntera*, orange in the female. It is, however, white in the large majority of specimens that I have seen.

† This statement as to the difference between European and American specimens of *P. atalanta* is made on the authority of Doubleday and Westwood (*op. cit.*, vol. i., p. 204), quoting Stephens. A specimen in the Hope Collection, labelled as from Illinois, in this respect resembles specimens from Europe.

of spots II. and the series III. which comes next outside it (fig. 4). The same appears with equal vividness in *A. sagana* ♀, and is plainly enough, though less strikingly, visible in the melanic *A. valesina* (fig. 27). The tendency to a lightening of the ground colour in this particular region appears again in *C. pantherata* (fig. 28), in this instance the ground colour being brown, though not so bright as in most brown Argynnis. Turning to *Argynnis diana* ♀, we find C indicated by a simple clearing up of the ground colour between the dark patches of series II. and III., and thus the present line of probable origin is seen to point in the same direction with those before suggested.

Although in the great majority of cases C is not specially distinguished from the general ground colour, except in the neighbourhood of the costa, yet there are some exceptions which must be noted, as they are of special interest. The yellow patch (C η , fig. 32) near the anal angle of the fore wing in *V. urticae* belongs to this series, as also the yellow shade at the costal margin of the hind wing in the same species. These are both recognisable in *V. polychloros*, and the latter in *V. io* plainly contributes to the pale zone surrounding the ocellus of the hind wing. But perhaps the most striking development of this series occurs in *A. sagana* ♀, where several members of the series are picked out in pale primrose. In the hind wing of this species a broad band is thus formed, which at once suggests the band that crosses the hind wing in so many species of the genera *Apatura* and *Limenitis* (figs. 29, 30). That the band in *Limenitis* corresponds with that in *Apatura* will scarcely be questioned, and that the band in *Apatura* exactly coincides in position with C θ — ξ in *A. sagana* ♀ will be evident on a comparison of the latter insect with *A. ilia*, in which the spots of series III. are persistent.* The apparent continuation of the same white band on the fore wing of *Apatura* and *Limenitis* would also appear to be the counterpart of C ε — η in *A. sagana* ♀, and we are thus led to conjecture that both *Apatura* and *Limenitis* may have taken their origin from a form like the present.

* As they are also in some other species of *Apatura*, e.g., *A. celtis* and *A. clyton*.

4. *The dark area between C and D.*—Having traced C and D throughout many of the species of the group, we shall, of course, find it easy to identify the dark area included between C and D in the same insects.

On the upper surface of the fore wing in *P. cardui* and *P. atalanta*, this dark area simply partakes of the general black or dark brown of the ground colour of that part of the wing, and shows no tendency to break up into separate constituents.

In *V. io* the same area is easily recognised as forming the centre of the ocellus in the fore wing, and a part of it is here suffused with the ruddy chestnut of the general ground colour.

In *V. urticae* this area somewhat resembles in shape the same area in *V. io*, but is sharply marked off from the red ground colour. *V. polychloros* shows us the same dark patch, in many cases breaking up into a chain of spots which run parallel with the submarginal series IV. and the hind border of the wing. Much the same appearance is presented throughout the genus *Grapta*, but in *Grapta c-aureum* we find the suggestion of a breaking up of the area into two lateral constituents by the inclusion of a patch of the ordinary ground colour just internal to D α . This resolution is faintly indicated on the under side of some of the species we have already noticed by a paling of the ground colour towards the middle of the patch. Turning now to the genus *Argynnis*, we find, as before, the same arrangement in a more simple and intelligible form. The dark area is completely resolved into dark spots, situated on the ordinary ground colour, and falling into two series, an inner and an outer. The outer series is clearly seen to be the first part of a chain of eight spots, running right across the wing to the inner border, generally parallel with series IV., but with a decided inwards curve opposite the middle of the hind border. This is the series I have named III. It is, of course, one of the most constant and characteristic features of the pattern of the ordinary Argynnids.

The inner constituent is a triangular or crescentic patch, usually an obtuse-angled triangle, with its base at the costa, and its apex pointing backwards and outwards. This I distinguish by the sign III'. (fig. 31, cf. 4, 27). It is generally large and well-marked in the

females throughout the genus *Argynnis* (including *A. sagana* and *A. niphe*) ; in the males it is smaller, often crescentic instead of triangular, and sometimes (as in *A. paphia* ♀), apparently on the point of disappearance. In *Clothilda pantherata* ♂ ♀ it is resolved into a series of three (sometimes four) dark spots, converging with III. 1—5 towards the middle point of series III. (fig. 28). The same condition obtains in *A. diana* ♀, except that here the dark spots are less sharply differentiated from the rest of the wing.

We see accordingly that the dark space between C and D in the genera *Pyrameis* and *Vanessa* forms part of a series. This series occurs in its least modified and most complete form in the genus *Argynnis*, where it consists of a chain of dark spots, in their origin undoubtedly, like series IV., survivals of the primitive dark ground colour (see *A. diana* ♀) extending the whole way across the wing nearly parallel to the hind border, and giving off in the interspace between the 3rd median and 2nd discoidal nervules an interior branch which reaches the costa separately (fig. 31, III., III').

In the genera *Pyrameis*, *Vanessa* and *Grapta*, the spots posterior to the point of bifurcation have generally disappeared, while the two branches III' and III. are usually fused together with more or less admixture of the light ground colour* (figs. 1, 2, 3).

The question may suggest itself whether the two small black spots near the middle of the fore wing in *V. urticae* (fig. 32, II. 6, 7) do not represent two terms of this series. They are clearly identical with the two larger spots in the similar situation in *V. polychloros* (fig. 33), and these again with spots constantly present in the genus *Grapta*.

If we examine the fore wing of a specimen of *V.*

* Before leaving the subject of series III. with its offshoot III', we may notice that the first one or two members of III. show a strong tendency to approach and become fused with the corresponding members of IV. (clearly seen in figs. 4, 31). The interval between the fore part of III' and III. thus becomes better marked than that between III. and IV., and it is this interval that gives rise to *a* in series D, which thus constitutes an exception to the general relations of its series. This is most clearly shown by *A. nerippe*, in which *a* is conspicuously picked out in white on the usual tawny ground colour of an ordinary *Argynnis*, and is well seen to belong to the interval between III' and III.

polychloros in which resolution of III. is pretty well marked, we shall find the constituents of III., together with these two spots and the large spot at the anal angle of the wing, forming a regular series in the form of an S. Comparing such a specimen with any *Argynnis*, we shall be tempted to indentify this series as a whole with series III. in the *Argynnis*, the only conspicuous difference being that in the latter the curve is less pronounced. With regard to the large spot at the anal angle I have no doubt of the correctness of the identification. It exactly represents in *V. polychloros* the spot III. 8 in the Fritillaries. The two others, however, do not really represent III. 6 and 7 as they seem to do; but belong to another series, the history of which will be traced later. This is shown by a careful examination of *Grapta c-aureum*, in which the two spots corresponding to those in *V. polychloros* are plainly seen, while outside them come two minute but unmistakable representatives of III. 6 and III. 7 (fig. 34). If any one doubts this, he has only to look at the underside, where he will find the whole of series III., with its branch III', sharply indicated by small black dots, two of which coincide exactly with III. 6 and 7 on the upper surface, while the representatives of the other two spots in question lie well to the inside of the present series. A feature in *G. c-aureum* worthy of notice is the presence in III. 7 (upper surface) of a minute patch of blue scales (the import of which will be explained later), indicating that it is in series with the blue centred III. 8.

It is interesting to observe that, as shown by the case of *V. polychloros*, it is possible for a new series to be made up out of parts of two old ones.

Series III., like the already described series IV., extends into the hind wing, here constituting a chain of spots most usually five in number, occupying the five interspaces from the 1st subcostal to the 1st median nervule. These five spots I distinguish by the numbers III., 10—14. They are conspicuously present in *P. cardui* (fig. 24), both upper and under surface; in the latter situation appearing as extremely handsome ocelli. They are present but less conspicuous on the under surface of *P. atalanta*; on the upper surface of this species they are partly obscured by the prevailing dark

ground colour, but still can in most specimens be easily distinguished by a careful examination. In *V. urticae* and *V. polychloros* they are absent from both surfaces, so also almost entirely from the under surface of *V. io*, where, however, in some specimens, vestiges of III. 10 and 11 can be traced. In the genus *Grapta*, the spots of this series on the upper surface, as a rule, are fused; and the series appears as an irregular brown band, darker than the general ground colour, but paler than the spots of another series (II.) which at present remains undescribed. On the under surface in this genus, the spots are often discrete and pretty easily recognisable; this is notably the case in *G. e-album*.*

In the genus *Argynnis* we find, as we should expect, the spots of this part of the series constantly present and very distinct, especially on the upper surface (fig. 31). Beneath, they may be conspicuous as in *A. adippe* and *A. lathonia*, where they are picked out with silver, present but somewhat faintly distinguished as in *A. paphia*, or modified into mere patches of green shading to the silver spots, as in *A. aglaia*. The series in *A. lathonia* is reinforced by the presence of III. 9 and III. 15, which in most species are wanting; and the under side of this insect gives perhaps the most complete view of the whole series that can be found in the genus. In *A. diana* the spots are present but small, in the male almost evanescent, and in both sexes absent from the under surface.

Two points of interest remain to be noticed before the present series is dismissed. The first is the relative size of the spots III. 10—14.

In the genus *Argynnis*, III. 12 is almost always smaller than the rest, it may even disappear altogether, as often in *A. adippe* ♂. In the genus *Pyrameis*, III. 11 and 14 show a strong tendency to exceed the average size. This is well seen on the under side of *P. atalanta* (less clearly in *P. callirrhoe* and *P. gonerilla*), and on both surfaces of *P. cardui*. In *P. huntera* the enlargement of these two members of the series becomes a very conspicuous feature of the pattern, the under side in this species often presenting III. 11 and 14 in the

* In *G. e-aureum*, III. is very well defined in the hind wing, where the spots composing it are blue-centred (see p. 114).

form of two large and very showy ocelli, while the rest of the series is almost or quite obliterated.

The conspicuous ocellus near the anal angle of the hind wing in *A. iris* (fig. 30) may very probably be identified with III. 14, as is shown by a comparison of the under side with that of *A. ilia*, in which most of the series is present.

The second point that remains for notice is the frequent occurrence of blue centres in the spots of this series. A large proportion of British specimens of *P. cardui* have a few blue scales in the centre of III. 14; in some there are distinct blue patches in the centre of both III. 13 and 14, while specimens of *P. kershawi*, from S. Australia, have conspicuous blue centres to these, and also to III. 12 in addition. It is interesting to remark that (so far as I have observed) those British specimens of *P. cardui* in which $D\epsilon$ is present, mostly have blue centres to III. 13 and III. 14 as well*; as we know that the presence of $D\epsilon$ is an ancestral feature, this would lead us to make further enquiry into the occurrence of these blue centres, in order to see whether they too have a history. Turning to the closely allied *P. huntera*, we find the blue centre well-marked in III. 11 and 14, while in *P. carye* we find the whole series in the hind wing blue-centred, with the exception of III. 10. In the very showy *P. gonerilla* of N. Zealand, III. 11—14 are conspicuously present on the upper side, each with a blue centre (fig. 25). *P. itea* has III. 12—14 provided with small blue centres, besides possessing a blue relic of IV. 15 at the anal angle of the hind wing. But the most interesting development of the blue-centred III. 10—12 occurs in *V. io*, where these three spots, without losing their separate identity, combine to form the ocellus of the hind wing. In many specimens of *V. io*, attentive examination of the hind wing will disclose the presence of the next member of the series, namely III. 13, in a rudimentary form, consisting in fact merely of a minute black patch, with a few blue scales in the centre, almost concealed by the long chestnut-coloured hairs that beset this part of the wing (fig. 35, III. 13). In the

* This, however, appears not to be the case with the British Museum specimen of *P. cardui* mentioned on p. 93, in which respect it differs from the Morteboe specimen mentioned on the same page.

'Entomologist' (Vol. xxii. (1889) p. 218; and Plate VIII., fig. 8), Mr. South figures and describes a variety of *V. io*, in which III. 10 and III. 11 remain distinct as simple black blue-centred spots, like the same spots in *P. gonerilla*,—this again confirming the account of the homology of the ocellus just given. The condition is represented in fig. 36.* Whether other materials enter into the composition of the central area of the ocellus in *V. io* I do not feel certain, but the appearance of the three blue constituents, especially the doubling of the middle one, would suggest that perhaps the sub-marginal blue-centred band IV. (cf. *V. urticae*) may have helped in its formation. I am, however, unable to bring forward any facts in support of this suggestion.

The blue centres to the spots of this series are not confined to the genera *Pyrameis* and *Vanessa*, but occur also in the allied genera *Grapta* and *Eurema*. In *Grapta c-aureum* not only are the spots in the hind wing blue-centred, but III. 7 and 8 (the former being rudimentary) in the fore wing are blue-centred as well. It will be remembered that this feature enabled us to decide upon the true position of the central black spots in the fore wings of *Grapta* generally, and so also of *V. polychloros* and *V. urticae*. In *E. dione*, III. 13 and 14 have distinct blue centres.

It appears then, to summarise the foregoing, that the present series (III.) has a history broadly corresponding with that of the previously considered (IV.), existing in its more generalised condition among the Argynnids, and in a form specialised by alteration and partial suppression in the Vanessids. Unlike the blue centres of series IV., which we saw to have a continuous history from the original ground colour of the Argynnids, the blue centres of the present series would appear not to be traceable further back than to the common ancestor of *Vanessa*, *Pyrameis*, *Eurema* and *Grapta*. They represent an added feature.

5. *The dark area between B and C.*—On the costa of the fore wing of *P. atalanta*, internal to the white band which I have called C, and external to the red band the costal termination of which I have marked as B, we find

* Taken, by kind permission of Mr. South, from the 'Entomologist,' *loc. cit.*

a black area, continuous posteriorly to C with the black ground colour that pervades the whole region of the apex. This is clearly identical with the central of the three black costal patches in *Vanessa urticae*, *V. poly-chloros*, and *Grapta c-album*, and is without difficulty also recognisable in *V. io* as the black claw-shaped mark which forms by its concave border the inner boundary of the ocellus (figs. 1, 2, 3, II.). On the underside of *P. atalanta* we find this surface diversified by certain bluish marks, of variable character, but on the whole tending towards a threefold division of the dark area in question. Turning to *Pyrameis cardui* and its immediate allies, we find no difficulty at all in identifying this area; and a glance at the under side of *P. cardui* or *P. huntera* enables us at once to recognise that here the threefold division visible in *P. atalanta* meets us again. The division between the outer and middle portion of the patch, however, is of far less importance than that between the middle and inner; and referring back to the upper side of *P. cardui* we see this latter division alone represented.

Of the two members into which this patch accordingly divides, the outer becomes merged in the dark ground colour of the apex, while the inner comes to an end near the origin of the 3rd median nervule, having enclosed the disco-cellular nervules in its course, and so having intruded a little way into the discoidal cell.* With these two landmarks to guide us, *viz.*, on the outer side C, and on the inner the disco-cellular nervules, we find it easy to mark out the corresponding area in the Argynnyids (fig. 4). As we should expect, we find here resolution instead of fusion; the twofold division is in most cases very clearly marked; the outer division, that immediately bounding C on its inner side, being clearly the beginning of a series of spots† (II.) which runs through both wings, upper and lower, and being separated by a region of the lighter ground colour from the inner division (II.') which, as in *Pyrameis*, just occupies both sides of the disco-cellular nervules (fig. 37).

Up to this point we have met with no difficulty in the

* This portion within the cell, however, belongs properly to another series (I).—*Vid. infra*, p. 118.

† Visible also on the under side of a specimen of *P. cardui*, from North America, in the Hope Collection.

investigation of this series, nor so far as the Argynnids are concerned does the least doubt arise with reference to the identification of series II., which occurs throughout the group just as universally as series III. and IV., and is traceable through both fore and hind wings with equal certainty* (fig. 37).

Nor, again, is there any room for doubt as to the presence of series II. in the hind wing of the genus *Pyrameis*; a comparison of *Pyrameis cardui*, *huntera*, or *myrinna*, with any *Argynnis* being conclusive on this point; though here the tendency towards fusion of the spots into a band is still more strongly marked than in *Argynnis*. The marginal region of the dark base of the hind wing in *V. urticae* and *V. polychloros* similarly results from the fusion of series II.; and the same feature is readily recognised in *V. io*, forming the dark crescentic border of the basal portion of the hind wing adjacent to the ocellus. In *Argynnis sagana* ♀, the homologous feature is the dark portion of the hind wing just internal to the broad cream-coloured band; in all probability corresponding with the similar character in *A. iris* and *ilia*, *L. sibylla*, &c. The presence of the three series, II., III., and IV., in the hind wing in an almost unmodified condition gives this region in *P. cardui* a great resemblance to the same in the Argynnids (cf. figs. 38, 39).

But with regard to the remainder of the series in the upper wing, considerable difficulty attends at present any attempt to bring the *Vanessa* and Argynnid types into harmony with each other; and though some of the steps in the reasoning that follows will not be disputed, the argument as a whole is somewhat doubtful, and must not be taken for more than it is worth.

The three black spots in the hinder portion of the fore wing in *V. urticae* are, as we have seen, certainly identical

* It is observable with regard to series II., as compared with III. and IV. in the Argynnids, that the spots of which it is composed (1) take a more zig-zag course across the wing, falling less easily into a regular series; (2) are themselves less circumscribed, often occupying the whole vertical space between two adjacent nervules, and thus tending, especially in the hind wing, to form a sinuous band rather than a chain of spots. In *A. diana* ♀ II. is present in its entirety, though not easily distinguishable from the general ground colour.

with the three similarly lettered in *V. polychloros* (figs. 32, 33; II. 6, 7, 8). The same three occur throughout the genus *Grapta*; in *G. c-aureum*, as has been seen, side by side with spots undoubtedly representing series III. (fig. 34). In *Grapta* we also get a representative of the spot at the anal angle of the fore wing in *V. polychloros*, which we have identified as III. 8. So far there is no difficulty. Now turning to *A. levana*, we may, I think, satisfy ourselves on a careful comparison with any *Grapta*, that II., 6, 7, and 8 are present, as well as III., 6, 7, 8; moreover, that there exist in *A. levana* two additional black areas in the angles between the submedian and median nervures, and between the 1st and 2nd median nervules, i.e., in the roots of the 7th and 8th interspaces. These we may regard as in series with II'. 1—5, and may conveniently call II'. 7, and II'. 8 (fig. 40). The latter does not occur as a distinct spot in any *Grapta* with which I am acquainted; the former, however, is found in many species (e.g. *G. interrogationis*), also constantly in *V. v-album*, and sometimes in *V. polychloros* (as in a specimen in the Hope Collection, fig. 33). Having thus met with a tolerably generalised type in *A. levana*, and having used it to interpret this part of the series in the *Graptas* and *Tortoiseshells*, we shall find that we are able to trace from the same type two diverging lines, the first leading towards the genus *Pyrameis*, the other backwards, as we may suppose, towards the *Argynnids*. The best species to compare with *A. levana* for this purpose is *P. carye* (fig. 41), in which II. 6 and 7 will be found, forming a continuous band across the wing, connected in front with the anterior portion of series II., and behind with III. 8; while II'. 7 is seen to be similarly connected with II. 8 vertically; and also with II. 7 horizontally by a lateral streak following the course of the 1st median nervule. II. 8 is represented by a distinct but narrow patch connected with II'. 7, while a dark and not distinctly defined area at the root of the 8th interspace may stand for II'. 8. The passage from *P. carye* to *P. huntera* and *P. myrinna*, and through *P. kershawi*, *P. cardui* and *P. callirrhoe*, to *P. atalanta* and *P. gonerilla* is so easy that it is not necessary here to trace it in detail; the main features being the merging of II. 6 in the general dark ground colour, the paring down of II. 7 until it becomes

a mere projection on the summit of III. 8, the filling up of the valley between II. 7 and II'. 7, and (in *P. cardui* and *myrinna*) the disappearance or melting into II'. 8 of II. 8; to which must be added in *P. callirrhoe* the gradual overspreading of the wings by a dark ground colour advancing from the base, this feature reaching its highest development in *P. atalanta* and *P. gonerilla*.

If the identification of the spots already given be correct, they can of course be easily found in any ordinary *Argynnis*. The greatest doubt exists with reference to II'. 7 and II'. 8, which would seem to be usually absent. A spot corresponding to the former may, however, sometimes be seen in *A. lathonia* and *A. adippe* (as in specimens in the Hope Collection), while one in the position of the latter occurs normally in *A. lathonia* and *A. niphe*, and not infrequently in *A. childreni*, *A. idalia*, and other species of the genus. The present series is thus seen to constitute no exception to our general rule; and to be traceable as to its posterior portion with certainty, though as to its anterior with some doubt, from its earliest beginnings in such a form as *A. diana* ♀, where it is hardly to be distinguished from the general ground colour, through the more specialised *Argynnis* to the highly modified form it assumes in *Araschnia*, *Pyrameis*, *Grapta*, and *Vanessa*, the difficulty of identification in the latter genera arising, as in the former cases, partly from the suppression of some of the spots, and partly from the fusion of spots belonging to the same or different series.

6. *The markings within the discoidal cell*.—The last series of markings that calls for notice is that which occupies the discoidal cell in fore and hind wings, distinguished collectively as series I. These in the fore wing consist in their simplest form of five transverse marks, I. 1 being a small black patch in the angle between the subcostal and median nervures (fig. 4), I. 2 and 3 being united into a more or less complete ring (under side of *P. atalanta*, both sides of *A. adippe* and some other *Argynnis*, figs. 4, 42). It is probably the latter of these two marks that forms the innermost of the black costal patches in *V. polychloros*, *V. urticae*, and *V. io* (figs. 1, 2, I., cf. figs. 42, 43). I. 4 appears in most *Argynnis* as a curved band with its convexity outwards; in *P. cardui* as a process from the summit of II'. 7,

rarely reaching forwards to the subcostal nervure; in *P. atalanta* as a similar but blunter process, easily visible on the under side (fig. 42), but on the upper reduced to a mere irregularity of the dark inner boundary of the red streak. I. 5 is closely apposed to the disco-cellular nervules, with an occasional intercalated patch of lighter ground colour (as often in *A. adippe*), and forms the innermost portion of the middle dark costal patch in the *Vanessas* and *Graptas*.

The markings in the discoidal cell of the hind wing (I. 6—9) are normally four, or corresponding to I. 1, 2, 3 and 5. I. 6, like I. 1, occupies the angle between the principal nervures of the wing, *i. e.*, the subcostal and the median; I. 7 and 8 are often united into a more or less regular ring; I. 9, when present, consists of a narrow dark border to the disco-cellular nervules (fig. 44). These markings are, as we should expect, best seen in the *Argynnids*; in the *Vanessas* they are mostly merged in the dark ground tint that pervades the base of the wing. I. 6, 7 and 8, however, may be distinguished on the under surface of *V. polychloros*, *V. urticæ*, *V. io*, and other species.

7. *Phylogenetic conclusions*.—It now remains to put together the results of the preceding investigation, and to draw from them what conclusions seem possible as to the phylogeny of the forms examined.

It would appear, then, that all the lines which we have been able to trace converge in the direction of a dark olive or blue-coloured *Argynnid* like the female of the recent *A. diana*.* Possibly, were we able to go back further still, we should find a type in which the dark coloration was absolutely uniform, as it is over the basal region of the wings in *A. diana*, no differentiation into ground colour and spots having yet taken place. From such a type as the last mentioned, the earliest step in advance would be taken by the lightening of the ground colour in patches between the nervures, the original dark tint remaining as ill-defined streaks and

* "The stem-form of the *Nymphalidæ* must have possessed a caterpillar approximately of the form that is now presented to us by *Acræa* . . . *Acræa*, the *Heliconinæ*, *Argynnis* still remain in this stage of development." W. Müller, "Südamerikanische Nymphalidenraupen," Zool. Jahrbücher, Bd. i., p. 621. This is confirmatory of the primitive character of *Argynnis*.

spots between the lighter patches. This, as we have seen, is exactly the state of things now existing in *A. diana* ♀; and a consideration of this and other species (*A. idalia*, *A. leto*, &c.) will lead us to the conclusion that the process of differentiation began at the hind border of the wings, and has gradually extended inwards towards the body. Thus in *A. diana* ♀, we find the series of dark spots IV. and III. already distinguishable, though not yet well-defined, while II. is just emerging into separate existence.*

The four normal series of dark marks having thus been made distinct, as, for instance, in *A. paphia* var. *ralesina*, we find in the next place a very general alteration in the pale areas of the ground colour between the spots. This loses its dull olive or bluish tint and becomes bright brown, as in nearly all Argynnids, the spots at the same time becoming, as a rule, smaller and more sharply defined. The original ground colour, however, clings to the females of certain species, and even, though in a less degree, to the males. Among the female Argynnids which retain the primitive ground colour, there occurs the very striking form *A. sayana*, in

* Scudder (*op. cit.*, vol. i., pp. 513—515) advances the view that the dark coloration in butterflies began as a dark border to the wings, spreading inwards and breaking up. It does not appear from the passage cited whether Scudder would consider the spots in the Argynnids to have directly arisen in this way, though his language would seem to suggest such a conclusion. I myself believe the balance of probability to be in favour of the view taken in the text, for the following reasons:—(1). Other evidence seems to show that the darker Argynnids are the older. (2). The general prevalence of a dark colour at the *base* of the wings even in brown Argynnids indicates that this at least is an ancient feature. (3). The spots in series II. seem by their shape (*vid.* p. 116, note) to bear traces of their latter differentiation. Such species as *A. lathonia*, in which the spots of series II. are distinct and circumscribed, like those of series III., we should on other grounds consider as the more highly specialised members of their group. Higgins ("On the Colour-patterns of Butterflies," 'Journal of Science,' 1868, pp. 323—329), suggests that the arrangement of the dark markings depends on that of the nervures, from the immediate neighbourhood of which they appear always to take their rise; while the lighter ground colour of the wing, which may be more or less affected by a "blush," is independent of the nervures. He makes, however, no attempt to show any reason for the alleged connection between nervures and dark colouring. As a matter of fact, both kinds of markings, whether light or dark, may either follow the nervures or be independent of them.

which, while all the dark series keep their normal places, an entirely new effect is produced by the still further paling of the ground colour in certain situations, especially between II. and III., or that region of the wings which we have denoted by C. In this way definite light-coloured bands are produced, which may readily suggest the source whence the groups represented by *L. sibylla* and *A. iris* respectively may have derived their characteristic pure white markings, the correspondence of which with those in *A. sagana* can scarcely be accidental.* In the neighbourhood of the brown Argynnids we find the slightly divergent form *C. pantherata*, which in the breaking up of the patch of original ground colour III'. marks a point of specialisation not reached by any true *Argynnis*, while its somewhat dull ground colour, and the peculiar accentuation of the costal portion of C and D, relating it to *A. valesina* and *A. diana* ♀, would seem to indicate its early separation from the Argynnid stem. This accentuation of C and D is carried to a much greater extent in *A. niphe* ♀, one of those transitional species in which we see the old and new ground colour fighting for the mastery. In this conspicuous and highly ornamental species we seem to have reached the point at which those butterflies called in the wide sense Vanessas quit the parent stem.†

* W. Müller (*op. cit.*, p. 622) considers that the group including *Limenitis* (which he names "Rippenbauenden") must find its root either among the *Vanessinae* or the *Diademinae*. This would remove *Limenitis* a step further off the Argynnids than my own suggestion would warrant, though it accords with my conclusion as to their relative antiquity. The position of *Apatura* Müller owns to be a puzzle (*Ibid.*). He inclines to remove it from the group of "Rippenbauenden," and somewhat doubtfully suggests its enrolment among the *Vanessinae*, in the neighbourhood of the genus *Hypanartia* (*Eurema*). In favour of this it may be mentioned that (according to Scudder) the eggs of *Apatura* bear more resemblance to those of the *Vanessidae* and even of the *Argynnidae* than to those of *Limenitis*, and also that *Apatura* corresponds with many of the *Vanessidae* in having 2 rows of spines instead of 4 on the under side of the last tarsal joint. (Scudder, *op. cit.*, vol. i., pp. 227, 8).

† The above statement as to the relative antiquity of *Argynnis* and *Vanessa* is in accordance with Müller's conclusions derived from a study of the larvæ. "A multiplication of the rows of spines from 6 [as in *Argynnis*] to 9, and the addition of the Ds and Ped rows has led to the forms that the *Vanessinae* now show us." (*Op. cit.*, p. 621).

The earliest representatives of the group or subfamily *Vanessinæ* would seem before long to have separated into three divergent tribes, each pursuing a distinct path. In the first of these, that leading towards the genus *Pyrameis*, the decorative features of *A. niphe* are mostly preserved, and indeed, enhanced. The vivid contrast between the white portions of C and D and the surviving dark ground colour of the tip of the wing is rendered still more striking by the deepening of the ground colour to a dark brown or black, and the consequent blending of the spots belonging to the costal portion of III., III.' and IV. into a uniform dark area, on which the white constituents of D, now formed into definite spots, tell out with much effect (*P. cardui*, &c.). The newer and lighter ground colour is now sharply marked off from the older and darker, instead of gradually passing into it, and is, moreover, itself brightened up, especially in the anterior portion of the fore wing, into a fresh salmon colour, which in the most highly specialised members of the genus is further transformed into a brilliant scarlet (*P. atalanta* and *gonerilla*). The relics of bluish ground colour round the margin of the wings as in *A. niphe* are awakened into greater brilliancy and used in combination with the spots of series IV. to form an extremely handsome border to the wing. This feature, though from its presence in all three of our diverging subgroups we must suppose it to have belonged to the "Protovanessa," or common ancestor of the three, is in *Pyrameis*, as we have seen, already on the wane, remaining chiefly in the neighbourhood of the anal angle of the hind wing, and in some species contributing a blue infusion to the spots of series D. On the under side it persists, though in reduced splendour. It would seem also probable that the "Protovanessa" was furnished with blue centres to the spots of series III., persisting in *P. gonerilla*, *P. kershawi*, *P. terpsichore*, *P. carye*, and (sometimes) *P. cardui*. The correspondence described in detail on p. 117 between the remaining marks of *Pyrameis* and those of *A. levana* tends to the conclusion that *P. carye* is perhaps the *Pyrameis* that comes nearest to the "Protovanessa," and from this species as a central point it is easy to trace in one direction *P. terpsichore*, *P. huntera*, and *P. myrinna*; and in the other direction, *P. kershawi*, *P. cardui*, *P.*

callirrhoe (*P. indica*), *P. atalanta*, and *P. gonerilla*.* It is worthy of notice that *P. gonerilla* preserves the blue of III., which has been lost by *P. atalanta*, *P. callirrhoe*, and to a great extent by *P. cardui*, and that *P. atalanta* and *P. gonerilla* both preserve $D\epsilon$ (*P. atalanta* ♀, also $D\zeta$), which spots have with rare exceptions vanished from *P. cardui* and *P. kershawi*. $D\zeta$ is found in all the three species of the group headed by *P. terpsichore*. It is also interesting to note the different origin of the black ground colour on the inside and outside respectively of the scarlet streak in *P. atalanta* and *P. gonerilla*. That on the outside is a survival in an intensified form of the original dark colour of the primitive Argynnid, that on the inside is a new feature seen for the first time in *P. callirrhoe*, this part of the wing having in the history of the species been dark, light, and dark again. From the stem leading off from the "Protovanessa" towards the genus *Pyrameis* is emitted the branch represented by the genus *Eurema* (*Hypanartia*). *E. zabulina* bears a strong resemblance to *P. carye*, especially on the under side. *E. kefersteinii* is in some respects intermediate between *E. zabulina* and *E. dione*, this latter being probably the most highly specialised of the genus, though retaining series III. with its blue centres in the hind wing.

The second of the three lines diverging from the "Protovanessa" is that followed by the genus *Araschnia*, the single species composing which presents in a remarkable form, as is well known, the phenomenon of seasonal dimorphism. It is not necessary here to recapitulate the analysis of the markings of *A. levana*, which showed this form to be in some respects intermediate between the present members of the genus *Pyrameis* and the Argynnids; or to do more than mention two other features in which *A. levana* reproduces the characters of

* Prof. Meldola ('Weismann's Studies in Theory of Descent,' English ed., 1882, vol. 2, p. 447), arranges the genus *Pyrameis* in a somewhat different manner, as follows:—*P. atalanta*, *dejeanii*, *callirrhoe*, *tamamea*, *myrinna*, *huntera*, *terpsichore*, *carye*, *kershawi* and *cardui*. It appears to me, I confess, that the transition from *P. cardui* to *P. atalanta* through *P. callirrhoe* (*indica*) is complete, and that the continuity is broken by the interposition of *P. huntera* and *myrinna*. I am unfortunately not acquainted with *P. dejeanii*.

the common ancestors of the group, *i. e.*, the blue-centred series IV. and the white spots of series D. In this last particular the form *A. prorsa* comes nearer the ancestral type than *A. levana*; in all other respects, however, it bears marks of higher specialisation, and it is worth notice, as a confirmation, that Weismann* concludes on quite other grounds that *A. levana* is the older form.

The last line leads off through the genus *Grapta* to *Vanessa polychloros*, *urticæ*, *ichnusa*, and *milberti*, no doubt in the order given by Prof. Meldola.† The nearest approach to the "Protovanessa" among the Graptas is furnished, I believe, by *G. c-aureum*. This interesting form by its aspect at once recalls the Argynnids, both in colour and markings. As we have seen, it is characterised by the possession of several ancestral features, for example, the co-existence of series II. and III. in the hinder part of the fore wing, and the presence of blue centres in the latter throughout its extent. The affinity of *Grapta* to *Araschnia* is suggested by the markings (especially the occurrence in both of the series II.), and is supported by the fact that the larvæ of both genera are distinguished among their allies by the occurrence of two spines on the head. The blue centres of series IV. in *V. polychloros*, improved upon in *V. urticæ*, are an ancestral feature that has mostly disappeared from the upper side of the Graptas, though still, as a rule, recognisable beneath. A noticeable characteristic of the present group is the gradual disappearance of series III. Well represented in *G. c-aureum*, where it preserves the blue centres of the "Protovanessa," it loses in the rest of the genus its distinct character; in *V. polychloros* it cannot be traced in the hind wing or in the middle of the fore wing; while in *V. urticæ* the outermost costal patch is its only remaining vestige.

Somewhere probably near the beginning of this third stem came off a branch, which ends in the two species *V. antiopa* and *V. io*. Both of these forms preserve the ancestral blue-centred black border; *V. antiopa* in completeness, *V. io* partly as a constituent of the ocellus of

* 'Studies in the Theory of Descent,' vol. i., p. 19.

† "*C-album*, *i-album*, *v-album*, *faunus*, *comma*, *dryas*, *polychloros*, *xanthomelas*, *cashmirensis*, *urticæ*, *milberti*." Weismann, 'Studies, &c.,' vol. ii., p. 447, note.

the fore wing, partly as an almost invisible rudiment. The latter species preserves series D in a conspicuous form, to which, indeed, it owes much of its beauty; and it also bears another, though less ancient, mark of descent in the presence of series III. with its blue centres in the hind wing; this again partly appearing as the finely-developed ocellus, partly existing only as a rudiment, which cannot be seen without the closest examination.*

In conclusion, it need scarcely be said that the present paper makes no claim to completeness. Fresh lines of investigation which continually offered themselves during its progress have had to be deliberately passed over in order to keep the subject within bounds. I do claim, however, to have broken new ground in a wide field. And while I hope to return to this field on a future occasion, whether with the present or other families, I trust that what I have now put on record may be taken as a contribution towards a natural and rational arrangement of the Argynnids and *Vanessidæ*.

I have to offer my grateful acknowledgments to Prof. Westwood for his kindness in allowing me free access to the Hope Collection at Oxford under his charge, and in affording me every means for working in his department, together with other help of various kinds. I am also under great obligations to my friends Dr. G. B. Longstaff, Mr. W. Hatchett Jackson, and Mr. E. B. Poulton, F.R.S., for much information and many valuable suggestions, for which I here wish to tender them my sincere thanks.

Postscript.

Since the foregoing paper was written a communication by Van Bemmelen† has appeared in the 'Tijdschrift der Nederlandsche Dierkundige Vereeniging,' in which the author gives the result of some observations made

* It is worth noting that the blue of the ocellus of the fore wing and that of the hind wing have different origins. The latter traces back to the "Protovanessa" only, the former to the ground colour of the primitive Argynnids.

† "Ueber die Entwicklung d. Farben und Adern a. d. Schmetterlings Flügeln." 'Tijdsch. d. Nederl. Dierk. Vereen.,' 2nd serie, Deel II., Aflevering 4, Leyden, 1889, pp. 235—247.

by him on the pupal and imaginal wing-patterns of *V. urticae* and *P. cardui*, with the view of gaining some information on the question of their phylogeny. He finds that the wings in the pupal condition show a colour-pattern which differs in several respects from that finally assumed, and that the costal band and white spots in *P. cardui* (my C and D) are survivals of this primitive pattern. The series D in *P. cardui* originally extended as far as the interspace between the 1st and 2nd median nervules (my 8th interspace). He notices the occurrence of a variety of *P. cardui* possessing a fifth white spot (my D ε), and also speaks of a variety of *P. atalanta* with a small white spot in the middle of the red band, not seeming to be aware that this spot (my D ζ) is normally present in the female. Having drawn attention to the corresponding five white spots in *V. io*, he points out that the under side shows the rest of the primitive pattern as seven white dots in the dark ground colour; and that the under surface of the hind wing also possesses minute black dots representing spots which have disappeared from the upper surface, unless the ocellus results from the combination of the two anterior of them.* The fore wing in *V. polychloros* may also show the primitive row of light-coloured spots; the first two being united into a crescent shape, as in other *Vanessas*. This crescent, he proceeds (my D α), is the sole relic of the primitive row of spots in *V. urticae*, *G. c-album* and *V. antiopa*; in the last-named, however, the next spot (D β) takes part in the crescent as well. The series is also present in *A. levana* and *prorsa* (*op. cit.*, pp. 238—240). The author points out that the development of the wing-pattern in *V. urticae* confirms the conclusions derived from the same in *P. cardui* and from the imaginal forms cited. He describes the primitive pattern in the pupa of *V. urticae* as possessing

* V. Bemmelen does not clearly distinguish between series III. and IV., and I am not certain as to the identification of his dots on the under surface of the hind wing. Of the two series, IV. is by far the more easily recognisable on the under surface of the hind wing in *V. io*, being represented by large crescent-shaped spots, some of which may even have blue scales in their centres. As I have shown above (p. 113), the ocellus of the hind wing includes *three* not *two* members of series III., and the fourth is represented by a rudiment (fig. 35, III. 13), of which V. Bemmelen makes no mention.

the spots of my series D, which, however, disappear (with the exception of the first two) as the final pattern becomes established; and notices that the permanent black spots in the median interspaces (my II. 6 and 7) appear not in the place of, but on the inner (or midwards) side of the primitive light spots.

While entirely agreeing with Van Bemmelen as to the primitive character of the spots of my series D, I do not find myself able to concur with him in his conclusion that they are replaced or represented by the brown or black spots of the Argynnids (*op. cit.*, p. 240); nor do I consider that his opinion as to the primitive character of the markings in the *Danainæ* and *Satyridæ*, as compared with other *Nymphalinae*, is fully borne out by the facts (*ibid.*, p. 242). Nor again, for reasons given at length in my paper, can I fall in with the view that *P. atalanta* has on the whole undergone less alteration from the primitive condition than *P. cardui* (*ibid.*, p. 239), though this is no doubt the case with regard to the spots of series D.

Van Bemmelen, in the course of his communication, refers to a paper by C. Schäffer,* in which the latter writer mentions that he has at present been disappointed in his hopes of arriving at some phylogenetic results from a comparison of the final with the primitive pattern in the wings of butterflies, in the manner of Weismann's work on the colours of lepidopterous larvæ, and Eimer's on the colours of vertebrates. But the earliest stage observed by Schäffer (who also made use of *V. urticae* for this investigation) seemed to him to show already most of the characters of the final. He makes, however, in this connection, at least one remark of interest, *viz.*, that the pattern of the hind wings is longer in developing than that of the fore wings, and in this he is confirmed by Van Bemmelen. He moreover suggests that the submarginal band results from the fusion of separate spots, pointing (no doubt rightly) to its condition in *A. levana*, *P. cardui*, *P. atalanta*, and *P. gonerilla*,† and

* "Beiträge zur Histologie der Insekten." 'Zoolog. Jahrbüch.,' iii. (1889), pp. 611—652.

† With regard to *P. gonerilla*, Schäffer does not seem to have noticed that the distinct spots in the hind wing do not belong to the submarginal band (IV.), but to the next series (III.), as fully shown in my paper. The only indication of the submarginal band

the occasional signs of separation in *V. urticæ* and *V. polychloros* in support of this conclusion. Van Bemmelen holds the opposite opinion, considering an uninterrupted band in this situation more primitive than a series of spots. I need not here repeat my own conclusions on this matter, as they are sufficiently expressed in the course of the present paper.

Another recent treatise, mentioned by Van Bemmelen,* I have unfortunately not as yet been able to see.

EXPLANATION OF PLATES I., II., & III.

PLATE I.

FIG. 1. *V. urticæ*.

2. *V. io*.

3. *P. atalanta*.

4. *A. niphe*.

5. *P. cardui*.

6. *P. atalanta* ♂.

7. *P. atalanta* ♀.

8. *P. cardui*, var.

9. *P. huntera*.

10. *P. callirrhoe*.

11. *P. gonerilla*.

12. *V. io*.

13. *A. levana*.

14. *A. prorsa*.

15. *E. zabulina*.

16. *E. kefersteinii*.

17. *E. dione*.

18. *V. polychloros*.

on the upper surface of the hind wing in this species is the blue relic of IV. 15 (see fig. 25). The rest is merged in the general dark ground colour.

* Eimer, 'Die Artbildung und Verwandtschaft bei d. Schmetterlingen,' Jena, 1889.

PLATE II.

FIG. 19. *A. iris* ♀.20. *L. sibylla*.21. *A. paphia*, var. *valcsina*.22. *A. niphe* ♀, under side.23. *A. diana* ♀.24. *P. cardui*, var.25. *P. gonerilla*.26. *V. antiopa*.27. *A. paphia*, var. *valesina*.28. *C. pantherata* (series III. and III.' shaded).29. *A. sagana* ♀.

PLATE III.

30. *A. iris* ♀.31. *A. paphia* ♀.32. *V. urticæ*.33. *V. polychloros*.34. *G. c-aureum*.35. *V. io*.36. *V. io*, var.37. *A. adippe*.38. *P. cardui*.39. *A. paphia*.40. *A. levana*.41. *P. caryc*.42. *P. atalanta*, under side.43. *V. polychloros*, under side.44. *A. adippe*.

In all the figures the same letters and numbers stand for the corresponding markings, as fully explained in the text (see pp. 91, 92); *m*, median nervure of fore wing; *m*, do., hind wing; *sc*, subcostal nervure, fore wing; *sc*, do., hind wing; *b*, blue.

Each series (except A and I) has, for convenience, been considered to consist normally of 15 members, 8 in the fore wing, 7 in the hind wing, and the interspaces have received corresponding numbers. If it be borne in mind that the spaces between the median and submedian nervures in the fore wing and hind wing are invariably numbered 8 and 15 respectively, and that the others are numbered in succession from them, there will be no difficulty in using the system, though a slight want of correspondence between spaces and spots occurs near the extreme tip of the fore wing which may occasionally make it necessary to refer to the branches of the subcostal nervure by their separate names.